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Examensarbete i ämnet biologi
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Abstract

Elephants have long been recognized as important mediators of savannah vegetation structure. With their activities, like feeding on woody plants they may increase visibility of a habitat and produce coarse woody debris within that habitat. These changes in vegetation may influence major interactions between organisms, such as competition or even predation. I focused on the latter and experimentally tested the influence of elephant-induced vegetation changes on habitat and within-habitat scale risk. The experiment was performed in Hluhluwe-iMfolozi Park, South Africa on resource hot spots in savannah grasslands, i.e. grazing lawns. This controlled for resource availability and ensured sufficient herbivore visitation. I created experimental manipulations that should influence perceived predation risk at habitat and within-habitat scale. Firstly, I compared treatment plots with high and low visibility at habitat scale. I expected herbivores to prefer high visibility plots. Secondly, I added coarse woody debris (CWD) to both closed and open plot, at within-habitat scale. CWD may act as escape impediments or may decrease visibility and thus increase perceived predation risk. I expected herbivores to choose plots without CWD. Then I added predator scat to all treatment plots to introduce immediate predation risk which should additionally increase the perceived risk. I expected smaller, more vulnerable herbivores to respond stronger to immediate risk than larger ones. Herbivore response, i.e. visitation, occupancy and herd size, to risk manipulations was monitored with camera traps. Impala and warthog reduced visitation of plots with coarse woody debris, suggesting they perceived risk at within-habitat scale. However, the response of impala was strongly dependent on presence of predator scat and time of day – impala only reduced visitation to plots with CWD at night and when risk was immediate. Warthog avoided lawn edges and impala did as well at night, but increased the visitation of closed plots without CWD during the day. These responses show the variation in perception of habitat scale risk of different prey species. White rhino did not respond clearly to within-habitat or habitat scale risk, which provides unique experimental evidence that this megaherbivore may indeed be relatively invulnerable to predation. My results show that elephant induced vegetation changes influence both fine scale and habitat scale predation risk, however the smaller herbivore species perceive risk differently than larger ones and the perceived risk changes in presence of predator cues.

Introduction

"After man himself, probably no other animal has had as great an effect on African habitats as the African bush elephant, Loxodonta a. africana Blumenbac*."* (Laws 1970)

Elephants are well known for their profound effects on the environment. Digging for water, dust and minerals leaves behind large holes and pits, trampling near waterholes, migration routes and feeding areas exposes bare ground, discarding coarse woody material while feeding alters litter and nutrient dynamics (Haynes 2012). Even piling up dung and smoothing rocks were recognized as landscape significances (Kerley and Landman 2006).

The impact of elephant activity, including feeding, on woody vegetation i.e. coppicing, debarking uprooting and breaking trees and shrubs, has been intensively studied (Trollope, Trollope et al. 1998, Guldemond and Van Aarde 2008, Shannon, Thaker et al. 2011, Valeix, Fritz et al. 2011, Haynes 2012). Specifically, elephants have been recognized as "ecosystem engineers", re-shaping the terrain and thus creating, modifying and maintaining habitats for other species (Jones, Lawton et al. 1994).

Impacts of elephant activity on woody plants can have both positive and negative effects on the ecosystem, depending on the spatial and temporal scale of their actions and environmental factors such as rainfall (Guldemond and Van Aarde 2008). At moderate densities, elephants may be an important biotic regulators of tree-grass ratios and together with fire they maintain the openness of the savannah (Sankaran, Augustine et al. 2013) or even promote creation of grasslands (Laws 1970, Guldemond and Van Aarde 2008). On a landscape scale, such engineering leads to higher habitat complexity, creating a mosaic of unmodified and modified patches, which in turn increases species richness (Jones, Lawton et al. 1997, Wright and Jones 2004). Over time, these effects generate higher landscape dynamics in terms of changing habitats, species composition and resource accessibility. On the other hand, engineering on smaller scales and at a given time can lead to degradation of a certain habitat which may be detrimental for survival of certain organisms (Jones, Lawton et al. 1997, Kerley and Landman 2006, Valeix, Fritz et al. 2011). In high densities, elephants can have severe impacts on woody vegetation, which not only drastically reduces tree cover but can also have cascading effects through the whole ecosystem. Such scenarios seem particularly likely in any of Africa's fenced reserves that i) prevent elephant populations to expand their range outside the borders and ii) keeps populations free of human intervention (poaching, culling) (Laws 1970). Negative consequences of increased elephant densities on woody vegetation have been reported repeatedly (Kerley and Landman 2006, Guldemond and Van Aarde 2008, Valeix, Fritz et al. 2008, Boundja and Midgley 2010).

The impact of elephants on vegetation dynamics may mediate interactions among organisms (Jones, Lawton et al. 1997). A clear example of such vegetation-mediated effects is the possible influence of elephants on predation risk (Tambling, Minnie et al. 2013).

Several studies have shown that woody cover strongly affects predation risk perceived by ungulate prey, e.g. Mysterud and Østbye (1999) and elephant-driven shift between closed to open habitat can thus have a pronounced effect on large scale predation risk (Valeix, Fritz et al. 2011). The direction of these impacts differ between species, depending on their antipredation strategy – some species take advantage of cover to hide from predators ("hiders") while other species, that rely on flight strategy ("runners"), avoid thick vegetation and select for open habitats (Ripple and Beschta 2004, Caro 2005, Burkepile, Burns et al. 2013). For example, a study by Valeix et al. (2011) showed that elephant-induced structural changes in vegetation increased visibility which in turn decreased perceived predation risk for ungulates such as impala and steenbok. On the other hand, Tambling, Minnie et al. (2013) showed elephant-induced thicket fragmentation increased predation risk for small prey (such as duiker and bushbuck) since it enabled easier access for apex predators such as lion and hyena.

Although previous studies focused on the effect of elephants on habitat scale predation risk, elephants may also mediate fine-scale, i.e. within-habitat scale predation risk. As mentioned above, elephants generate coarse woody debris (CWD). A few studies from temperate systems have recently dealt with impacts of CWD as escape impediments (Halofsky and Ripple 2008, Kuijper, de Kleine et al. 2013). These studies suggest CWD induces strong herbivore response at a fine-scale (up to a few meters) because it limits prey escape possibilities from predators. Elephant-induced CWD in savannah system may thus either act as an escape impediment or even as a visibility obstruction, increasing predation risk at the within-habitat scale. Moreover, these effects could potentially counteract the effect of elephant on large, i.e. habitat scale risk. In other words, while opening up a wooded habitat may decrease predation risk of that patch, adding CWD may at the same time increase within-patch risk. In this thesis, I experimentally tested this assumption.

As mentioned above, several factors determine prey response to predation risk. One of the main characteristics determining the level of predation risk for ungulate species is their body size. In general, smaller herbivores are predated upon by a wider range of predators. A study by Owen-Smith and Mills (2008) showed herbivores weighing around 40 kg are the most common prey for all carnivore species of African savannah. The risk decreases for larger ungulates (Sinclair, Mduma et al. 2003) and the ones actively defending against their predators (Caro 2005). The largest herbivores, i.e. megaherbivores, weighing ≥1000 kg are the only group that is supposed to escape predation as adults and are rather regulated by the bottom-up ecological forces (Owensmith 1989, Hopcraft, Olff et al. 2010). Therefore, I expect this distinction to show in my experiment as well; smaller ungulate species should respond to elephant mediated changes in predation risk stronger than the larger species.

Another important aspect to consider is the temporal scale of risk. Habitat features allow prey to recognize risk on a long term scale, i.e. non favourable habitat would rather represent risk over a longer time period than it would act as a momentous threat, while direct predator cues give information about immediate predation risk. Predator odours such as naturally present scent markings, urine, faeces and fur and predators' vocalizations are

typical immediate risk cues and can easily be used for experimental manipulation (Nolte, Mason et al. 1994, Apfelbach, Blanchard et al. 2005, Favreau, Pays et al. 2013, Kuijper, Verwijmeren et al. 2014). I thus decided to include this aspect in my experiment and test whether herbivore response to habitat and within habitat scale risk changes in presence of immediate risk cue, i.e. predator scat.

Aim and Predictions

The aim of this study was to assess the impact of elephant induced vegetation modifications on predation risk at large, habitat-scale and fine, within-habitat scale. First, herbivore response to habitat-scale (degree of visibility) and versus within-habitat scale risk cues (presence or absence of CWD) was determined. Next, response of herbivores to the same risk cues was determined after increasing immediate predation risk through adding a natural predator cue (scat). Finally, the influence of an important abiotic variable, time of day, on perceived predation risk was determined and again, herbivore response assessed. From this sequence the following predictions were drawn:

1. At habitat scale, elephants reduce woody cover which may increase visibility and thus reduce predation risk at large scale
2. At within-habitat scale, elephants create CWD which may increase predation risk at fine scale
3. These effects will be especially strong when risk is immediate, i.e. presence of predator scat will additionally increase predation risk
4. Predation risk will differ between different times of day, i.e. higher at night then during the day
5. Predation risk will differ for different herbivore species, i.e. is highest for vulnerable, smaller prey species and lowest for biggest herbivores

Methods

Study area

I performed this study in Hluhluwe-iMfolozi Park (HiP), KwaZulu Natal, South Africa, that covers an area of approximately 900 km^2. The park is fenced along the entire boundary area. The landscape is hilly in the North (hilltops reach up to 750m) and relatively flat in the South (altitude of about 60m), with rivers and streams seasonally fluctuating in the water levels present throughout the whole park (Boundja and Midgley 2010). The climate differs across the park as well, with more rainfall in the northern part (up to 1000mm annually) and less in the South (up to 700mm annually) (Boundja and Midgley 2010). The majority of the precipitation occurs during summer. The area as a whole can be recognized as woodland savannah, a mosaic of grasslands and woodland, with scattered clusters of thickets (Trinkel, Ferguson et al. 2008).

Experimental Design

The whole experiment was repeated on 12 independent experimental units, i.e. grazing lawns (Fig 1) between April and August 2014 (more specifically from 14.4 to 11.8. 2014). Grazing lawns are an important component of savannah ecosystems, characterized by short stoloniferous grasses communities, tolerant to heavy grazing (McNaughton 1984, Owensmith 1989, Cromsigt and Olff 2008). Due to the structural characteristics of the grasses, nutritious tissues are tightly packed in small dimensions and provide highly concentrated plant biomass, giving increased food yield per bite, i.e. maximizing nutrient intake, being highly exploited by grazing herbivores (McNaughton 1984, Archibald 2008). Continuous intensive grazing, especially of white rhino (Waldram, Bond et al. 2008), is crucial for maintenance of such highly palatable patches so that the fast growing taller grass species do not prevail. Positive feedback between heavy grazing pressure and high palatability allows the grazing lawns to persist in the dynamic savannah system (Archibald 2008, Cromsigt and Olff 2008). The limitation of experimental set up to grazing lawns allowed for controlled food availability and provided with sufficient herbivore visitation. Since prey need to balance between resource intake and safety, their responses to risk on unlimited food patches should be stronger. The concept has been described as "risk allocation hypothesis" (Lima and Dill 1990, Brown, Laundre et al. 1999). Grazing lawns occur throughout the whole park, but can be divided into different types according to the dominant lawn species. In iMfolozi, those are bushveld signal grass (*Urochloa mosambicensis*) and curly leafed dropseed (*Sporobulus nitens*) and in Hluhluwe lesser crabgrass (*Digitaria longiflora)* and sweet smother grass (*Dactyloctenium australe*) (Vos 2010). Since grazing lawns in the southern part are more numerous and larger in size with consistent dominant lawn grasses (pers.obs.), experimental sites were limited to iMfolozi part of the park to guarantee comparability.

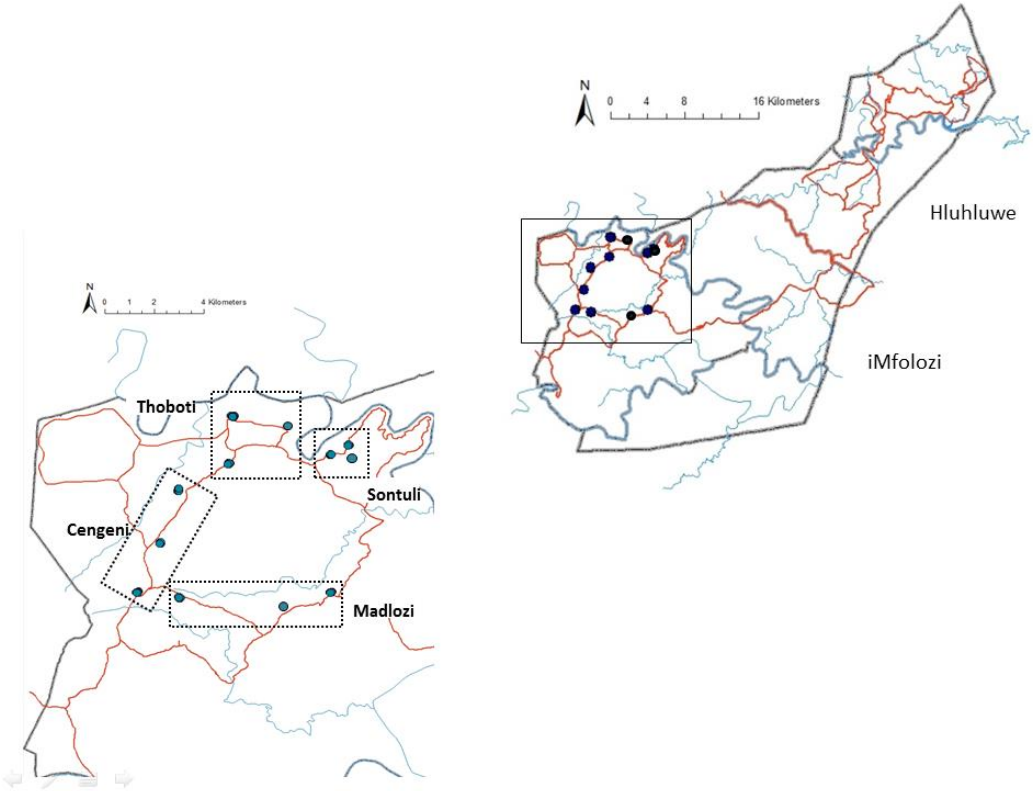

Figure 1 Map of Hluhluwe-iMfolozi Game Reserve (top right) with park boundaries in dark blue, major rivers in light blue and roads in red. The part of the park where the experiment was running is framed with a solid black line, showing locations of grazing lawns with dark circles, and enlarged (bottom left) for a detailed view. The detailed view shows the 4 areas where lawns were clustered. These areas were used as a random effect in the mixed-effects models.

All lawns were chosen according to the following criteria; a) distance from the road was at least 50 m, b) distance to water was at least 100 m, c) dominance of the same lawn grass species. Even though these restrictions allowed maximum comparison of the lawns, large scale landscape differences that could influence herbivore distribution between the areas where lawns were located, e.g. topography, overall herbivore density, big rivers and vegetation type, may still have been present. Therefore, the lawns were assigned to and grouped in four distinct areas of iMfolozi, which were more similar in these characteristics: Cengeni, Madlozi, Sontuli and Thoboti (Fig 1). These "areas" was included as a random effect in the statistical models (see section Statistical Analysis for more details).

Experimental treatments

In each lawn replicate, we set up 5×5 m plots with five separate treatments (Fig 2):

1. Control (C)
2. Presence of escape impediments (EI)
3. Scat control (S)

4. Decreased visibility (DV)
5. Decreased visibility and presence of escape impediments (DV&EI)

Figure 2 Photos of control plot (top left), plot with escape impediments (top right), plot with reduced natural visibility (bottom left) and plot with reduced visibility and escape impediments (bottom right). Scat plot was functionally the same as control plot during the no scat week and is thus not included. Stones were marking the corners and escape impediments always placed in three plot corners (the third escape impediment on both photos on the right is not entirely visible). Photos were all taken from the corner facing the camera trap.

Plots with reduced visibility (closed plots) were placed by the edge of the lawn, where thick bushland savannah started and provided a natural barrier for outlook. Others (open plots) were placed in the central part of the lawn where there was little or no woody vegetation. Coarse woody debris was placed in three of the corners of the plots mimicking elephant-induced escape impediments. The debris consisted of naturally present material available on or near the lawn – logs, bark and branches of roughly 50x50x100 cm high, wide and long, which are the dimensions used by Kuijper, de Kleine et al. (2013) . During the first week, the experimental set-up addressed the first objective, i.e. how do habitat characteristics (modified by elephant activity) alter herbivore perceived predation risk. Thus, scat control plot was functionally the same as the control plot in week one of data collection.

In the second week, predation risk was increased with addition of predator scat. Fresh scat (up to 10 hours after defecation) was collected by park personnel in advance and kept

frozen until used, either from free-ranging wild dogs in HiP or from wild dogs temporally kept in an enclosure within the park boundary for re-introduction elsewhere. A handful was added to all except the control plot after the first week of experiment and the experiment continued for another week with scat (Fig 3).

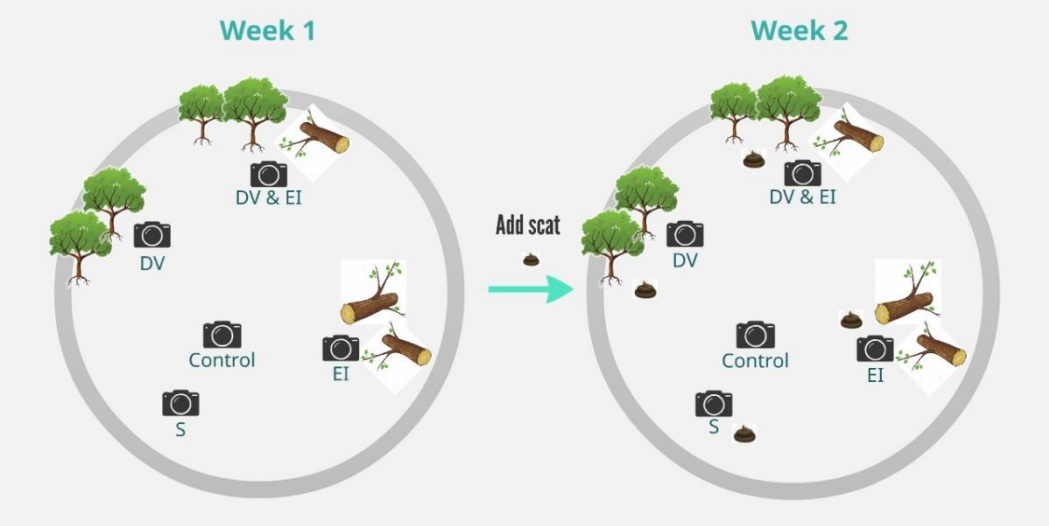

Figure 3 Scheme of an experimental set up with large circles representing one experimental replica (grazing lawn) over a course of 2 weeks. First week, I manipulated habitat characteristics (trees resemble reduced natural visibility and logs portray escape impediments). Then, I added scat (presented as such) to all except control plot. I measured herbivore response on each plot with a camera trap (presented with camera).

All treatment plots were spaced at least 10 m and not more than 80 m from each other so that individual animals could easily choose among different treatments. If there were any features on the grazing lawn that could cause aggregation of certain herbivore species, e.g. an active waterhole, well used walking path, a tree providing good shade and scratching posts like tree stumps or bigger rocks, plots were placed with a sufficient distance from them (at least 10 m). The corners of the plot were well marked (with small stones or branches) to make the plot borders visible on the camera trap data, however special care was taken the markings could not act as escape impediments as well (Fig 2). Camera trap was placed approximately a meter from the plot corner facing SW, to keep data collection consistent and to avoid receiving direct sunlight into the camera lenses. Cameras were either attached to a constructed pole or to a tree trunk, if available. For pragmatic reasons and to limit the duration of the whole study, I ran two experimental units at any given time. The first week of the second experimental unit began at the same time as the second week of the first experimental unit.

Recording ungulate visitation to treatment plots

I recorded animal visitation using Bushnell Trophy Cam HD camera traps, equipped with motion-activated PIR (passive infrared) day/night autosensor. Camera traps collected 30 s videos of animals visiting the plots. When animal activity was longer than 30 s, videos

were taken consequently with a second of lapse time. The following response variables were measured from each video using the software JWatcher 1.0:

i. **visitation**, defined as the number of herds of each species visiting the plots
ii. **occupancy**, defined as the duration that a herd visited a plot, in seconds
iii. **herd size**, defined as the number of individuals in a herd that visited the plot

Measuring herbaceous cover and visibility of each plot

Herbaceous cover and visibility were quantified for each lawn site and plot. First, vegetation was examined on each plot by identifying the grass and forb species and estimating their cover and greenness according to 6 different classes (Table 1). The measurements were taken in 16 0.5×0.5 quadrants per plot and the data was used to calculate relative cover of common lawn grass species and greenness of the whole plots. The experiment ran from the end of the wet season into the dry season and grass height was very short (≤ 7 cm, see Figure 2) and did not increase with time. Thus, grass height was not measured.

Table 1. Cover or greenness classes according to estimated percentage of cover or greenness per grass and forb species

Class	Cover or Greenness in %
1	0-10
2	11-25
3	26-50
4	51-75
5	76-90
6	91-100

Visibility was measured up to 20 m from the centre of each plot in all cardinal directions (N, NE, NW, S, SE, SW, E, W), using a 120 cm high, 20 cm wide white wooden visibility plank. The estimates were taken at 4 levels (0 cm, 50 cm, 100 cm and 150 cm for ground, warthog, impala and white rhino sight level, respectively) at a height of 40-60 cm, which is approximately the height of an approaching predator such as a wild dog or lion. Visibility measurements were done with two observers. I stayed in the centre of the treatment and the second person walked away from me, holding the visibility plank, in a straight line in each cardinal direction until the visibility was decreased for all levels or until he/she reached 20 m. Separately for each of the four sight levels, the null visibility was estimated by recording the distance at which at least 50% of the 40-60 cm plank section was no longer visible. To keep the measurements standardized I estimated all the visibility measurements.

Statistical Analysis

Vegetation traits

Factorial analysis of variance (ANOVA) was performed to check for differences in visibility between different experimental treatments for the different sight levels (ground, warthog, impala, white rhino).

Cover and greenness data was non-normally distributed and could not be transformed, so non-parametric Kruskal-Wallis was performed to compare the cover of the prevailing lawn grass species (*S. nitens* and *U. mosambicensis*) and greenness among different treatments.

Visitation, Herd Size and Occupancy

In total, 16 136 videos were extracted from the camera traps, of which 1 118 showed animals visiting the experimental plots. The rest either included animals appearing outside the treatment plots or were taken when camera was triggered by moving vegetation. The first lawn replica was discarded due to an excessive amount of missing data – I was still fine-tuning the methodology at that point.

Since most herbivore species using grazing lawns live in herds or groups and thus function as a unit herd rather than separate individuals (Lima and Dill 1990, Caro 2005), I used number of herds as response variable rather than individuals. All individuals of the same species appearing on footage in a time span of 15 min were defined as members of the same herd. I estimated the herd size for each herd counting the individual animals present in each video of that herd and then used the daily maximum value of those counts. Occupancy was estimated by summing the total time individuals spent on the plot. Concluding, I used herd visitation (number of herds per day), occupancy (time a herd spent on a plot) and maximum daily herd size as response variables and tested how these were affected by experimental treatments.

I also tested how treatment effects differed for time of day and different herbivore species. Time of day was defined by the times of sunset and sunrise, while accounting for the seasonal differences. Day and night were the periods of complete sunlight and darkness, respectively. Dusk was defined as the period of an hour before and after sunrise and dawn as the same time frame around sunset. Using four (day, dusk, night, dawn), or even three (day, night, crepuscular) levels for the "time of day" variable caused convergence problems, possibly due to the limited sample size. Therefore, dawn was joined with night and dusk with day, defining "night" and "day", respectively.

24 different species in 618 herds, or groups, were identified (Table 1). The three most common species visiting the grazing lawns were impala, white rhino (henceforth rhino) and warthog (Table 2, in bold). Unfortunately, numbers of other herbivore species were too low to be included into further analysis.

Table 2. Summarized data from camera trapping; the total number of different herds, or groups, is given per treatments along a declining visibility gradient (C, S, EI, V, DV&EI) for 24 species that visited the plots.

Species - common name	***Species - scientific name***	***C***	***S***	***EI***	***V***	***DV&EI***	***Total***
Impala	*Aepyceros melampus*	25	51	25	51	14	166
White rhinoceros	*Ceratotherium simum*	26	20	21	9	12	88
Common warthog	*Phacochoerus africanus*	27	17	9	7	10	70
Birds	*Aves*	12	16	29	6	2	65
Genet	*Genetta spp.*	6	2	8	10	11	37
White tailed mongoose	*Ichneumia albicauda*	12	14	3	4	3	36
Blue wildebeest	*Connochaetes taurinus*	8	10	3	4	3	28
Scrub hare	*Lepus saxatilis*	3	12	9	2	1	27
Black rhinoceros	*Diceros bicomis*	4	5	2	3	3	17
Giraffe	*Giraffa camelopardalis*	5	0	3	3	0	11
Aardvark	*Orycteropus afer*	3	2	2	1	1	9
African elephant	*Loxodonta africana*	2	3	2	2	0	9
Hyena	*Crocuta crocuta*	1	2	1	4	1	9
Greater kudu	*Tragelaphus strepsiceros*	1	1	0	4	2	8
Plain's zebra	*Equus quagga*	2	2	1	1	1	7
Chacma baboon	*Papio ursinus*	0	0	0	2	3	5
African buffalo	*Syncerus caffer*	2	0	0	0	3	5
Blue duiker	*Cephalophus monticola*	0	0	2	2	0	4
Vervet monkey	*Chlorocebus pygerythrus*	0	0	1	1	2	4
Common duiker	*Sylvicapra grimmia*	0	0	0	0	3	3
Lion	*Panthera leo*	1	0	0	1	1	3
Slender mongoose	*Galerella sanguinea*	0	0	0	2	1	3
Cape porcupine	*Hystrix africaeaustralis*	0	0	0	1	1	2
Cheetah	*Acinonyx jubatus*	0	0	1	0	0	1
Nyala	*Tragelaphus angasii*	1	0	0	0	0	1
Total		*141*	*157*	*122*	*120*	*78*	*618*

Differences in herbivore's response to experimental treatments were analysed using the statistical programme R 3.1.1 (R Core Team 2012) and the lme4 package (Bates, Maechler et al. 2014) for generalized linear mixed effects models (glmer).

The first two response variables (number of herds and herd size) consisted of discrete count data and I thus specified a Poisson family in the models. Occupancy was also non-normally distributed, but log transformation normalized the data (Shapiro-Wilk test; W=0.984, p=0.733 for Scat model and W=0.984, p=0.581 for Time of Day model – see below for model explanation).

Even though I had camera traps out for a week and aimed at collecting data for a full week, this was often not the case. Technical issues with the equipment, logistical problems in the park or interference of wildlife with camera traps (rhino or elephant knocking over the posts with camera traps), caused an uneven number of data collection days per treatment

plot. I corrected for this variation in number of sampling days, by calculating visitation as number of herds per day and by including the number of data collection days as random effect in the model. Moreover, lawn ID, area (one of the four general areas in which a grazing lawn was located) and week (first or second week of the experiment, with no scat or scat treatment, respectively) also acted as random effects and were included in all the models as a nested random effect (area/lawnID/week). This nested random effect corrected for potential spatial autocorrelation among lawn sites.

First, the overall effects of elephant impact treatments and adding scat together with their interaction were analysed (in a so called "Scat model"). Then, another ecologically important variable, time of day (night vs day) was introduced and analysed in a new "Time of Day model".

To assess the three way interaction between scat, elephant impact and time of day parameters, I first incorporated them in a model as individual fixed effects. However, an issue with convergence appeared, possibly due to the limited sample size. Therefore, I merged scat and elephant impact into one fixed effect with 10 treatment levels (five elephant impact levels * two scat levels). The second fixed effect for this model was time of day with two levels, day and night. Random effects for the Time of Day model were the same as for the Scat model.

The significance of the fixed effects for each species was determined by χ^2 statistics, using type III and type II ANOVA procedure for the full factorial model, including all the possible interactions between fixed effects. Model selection was performed afterwards to get the appropriate *p* values for effect sizes. Best adequate model (BAM) per species was chosen through comparison of Akaike's Information Criterion (AIC) values. The model with lowest AIC value, but at least 4 smaller than the one from the full factorial model, was selected for further analysis (Crawley 2007).

Results

Vegetation traits

Sight level ($F=23.85$, $p<0.001$) and experimental treatment ($F=223.5$, $p<0.001$) clearly affected visibility but the interaction between the two was not significant ($F=1.26$, $p=0.243$). The visibility at warthog, impala and rhino sight level was generally higher than at the ground level ($t=3.43$, $p=0.004$; $t=6.85$, $p<0.001$ and $t=7.39$, $p<0.001$ for warthog, impala and rhino, respectively) – visibility at warthog level was higher than at the ground level but lower than at impala and rhino sight level. Visibility did not differ between impala and rhino sight levels ($t=0.54$, $p=0.949$).

Visibility differed among treatments (Fig 4). The two treatments with high woody cover bordering the lawn indeed had the lowest visibility of all the treatments ($t=-21.51$, $p<0.001$ for plot DV and $t=-22.42$, $p<0.001$ for plot DV&EI). Open plot with escape impediments, though, also had lower visibility than the other open plots, but much higher visibility than the two closed plots ($t=-7.55$, $p<0.001$). This effect did not differ among different sight levels; the interaction between sight level and treatment was not significant (see above). There was no difference in visibility between the open control (C) and scat control (S) plot ($t=-1.66$, $p=0.461$) and between plots with reduced natural visibility ($t=-0.914$, $p=0.891$).

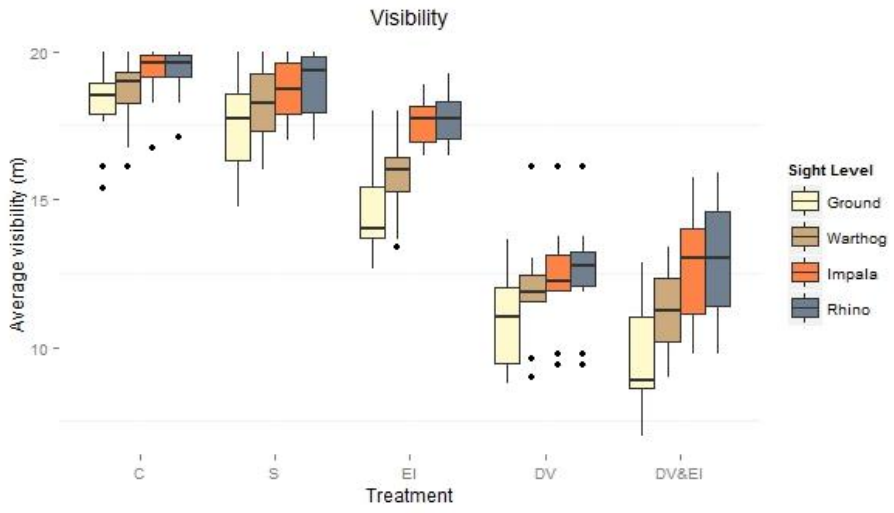

Figure 4 Boxplot of average visibility of experimental plots (C, S, EI, DV, DV&EI) for four different sight levels (ground, warthog, impala, rhino).

The cover of the prevailing lawn grass species (*Sporobulus nitens* and *Urochloa mosambicensis*) did not differ among the treatment plots ($\chi^2=5.12$, $p=0.276$ for *S. nitens* and $\chi^2=1.71$, $p=0.789$ for *U. mosambicensis*). The greenness of plots was also consistent among treatments ($\chi^2=4.00$, $p=0.406$).

Herbivore Response

Visitation

All species responded significantly to treatments mimicking elephant impact and in the case of impala this response was mediated by presence of scat (significant interaction Elephant impact × Scat, Table 2, Fig 5).

Table 2. Influence of elephant impact and scat treatment on number of herds visiting the experimental plots for impala, warthog and rhino.

Experimental treatment	***Impala***	***Warthog***	***Rhino***
Elephant impact	33.35 $_{(4)}^{***}$	16.16 $_{(4)}^{**}$	11.16 $_{(4)}^{*}$
Scat	0.23 $_{(1)}$	0.39 $_{(1)}$	0.01 $_{(1)}$
Elephant impact × Scat	9.71 $_{(4)}^{*}$	2.01 $_{(4)}$	2.08 $_{(4)}$

The table shows test statistics (χ^2 values) with degrees of freedom in parenthesis and significance levels (°, p<0.1; *, p<0.05; **, p<0.01; ***, p<0.001).

In the first week, when scat was not added yet, herds of impala avoided plots with escape impediments (EI and DV&EI). However, adding immediate predation risk in form of scat seemed to reverse this effects as more impala herds visited the open plot with escape impediments during the scat week (Table 3, p=0.052).

Warthog similarly visited escape impediment plots less but in contrast with impala also avoided low visibility plots in the first week of experiment, i.e. in absence of scat (Table 4). A different reaction to habitat characteristics was shown from rhinos. Less herds visited closed plots (DV and DV&EI), but rhino visitation was not influenced by escape impediments. Responses of warthog and rhino did not change when adding scat (Table 2).

Table 3. Effect sizes of elephant impact (escape impediments, decreased visibility and their interaction) and scat (scat vs no scat) on number of herds visiting the experimental plots for impala.

	Impala			
	Est	***SE***	***z***	***p***
Intercept (C)	-0.35	0.55	-0.64	0.521
EI	**-1.52**	0.54	-2.80	0.005**
S	0.42	0.36	1.15	0.249
DV	0.12	0.44	0.28	0.779
DV&EI	**-1.22**	0.56	-2.17	0.030*
C × Scat	-0.19	0.47	-0.41	0.680
EI × Scat	1.32	0.68	1.95	0.052$^{°}$
S × Scat	-0.68	0.56	-1.20	0.229
DV × Scat	0.41	0.57	0.71	0.480
DV&EI × Scat	0.05	0.75	0.07	0.945

The table shows test statistics (estimates (Est), standard errors (SE) and z values) and significance (°, p<0.1; *, p<0.05; **, p<0.01; ***, p<0.001) for the levels of the fixed effects, using the best adequate model for each species (see section Materials and Methods).

Table 4. Effect sizes of elephant impact (escape impediments, decreased visibility and their interaction) and scat (scat vs no scat) on number of herds visiting the experimental plots for warthog and rhino.

	Warthog				***Rhino***			
	Est	***SE***	***z***	***p***	***Est***	***SE***	***z***	***p***
Intercept (C)	0.02	0.41	0.04	0.969	-0.38	0.45	-0.83	0.406
EI	**-1.09**	0.38	-2.89	0.004**	-0.37	0.30	-1.23	0.218
S	-0.39	0.31	-1.25	0.211	-0.37	0.32	-1.17	0.243
DV	**-1.25**	0.42	-2.99	0.003**	**-1.15**	0.40	-2.89	0.004**
DV&EI	**-1.08**	0.38	-2.85	0.004**	**-0.93**	0.37	-2.52	0.012*
Intercept (C) × Scat	-0.17	0.25	-0.69	0.492	0.04	0.33	0.12	0.908

The table shows test statistics (estimates (Est), standard errors (SE) and z values) and significance (°, p<0.1; *, p<0.05; **, p<0.01; ***, p<0.001) for the levels of the fixed effects, using the best adequate model for each species (see section Materials and Methods). BAM did not include interaction of fixed effects.

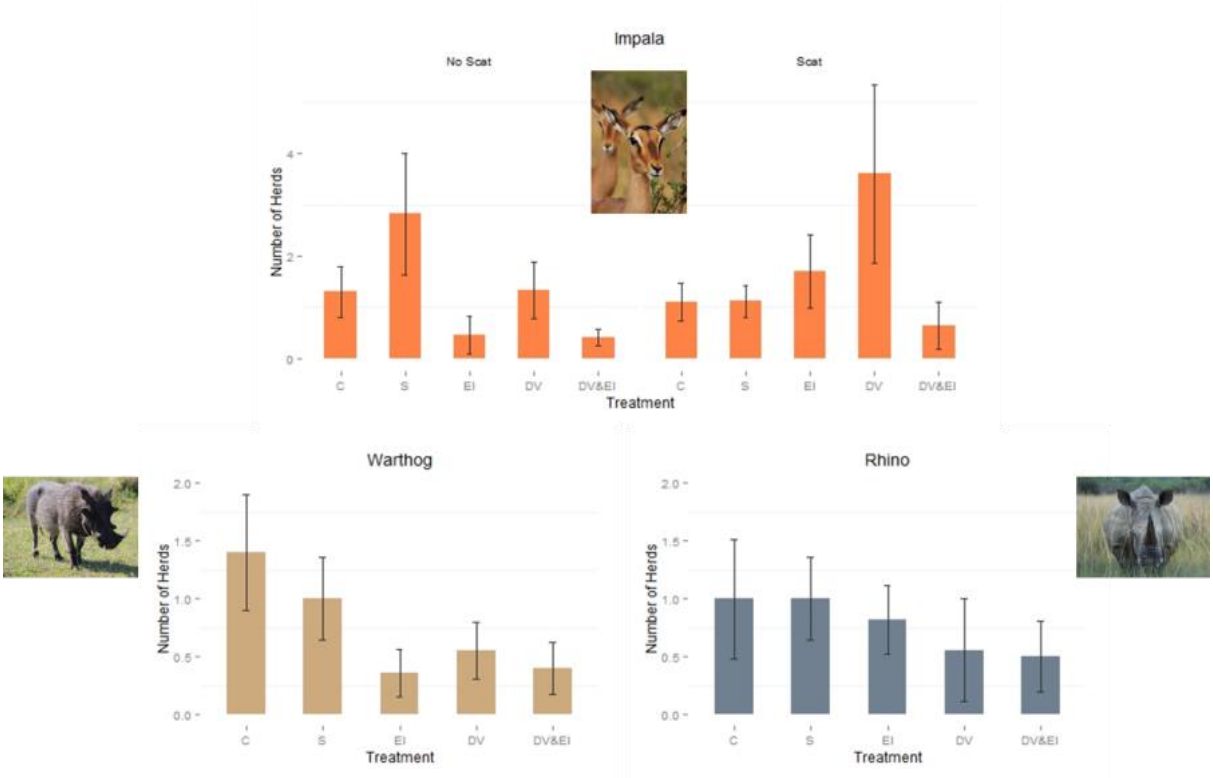

Figure 5 Visitation of the different experimental plots by impala (top), warthog (bottom left) and rhino (bottom right). Bars show average number of herds visiting plots of different treatments. Error bars reflect standard errors.

Herd Size

Elephant impact had a significant effect on the size of impala herds visiting the experimental plots and effects of elephant impact depended on presence of scat (significant interaction Elephant Impact × Scat, Table 5). The two other species did not show any variation in herd size in response to experimental treatments (Table 5).

Impala herds were smaller in plots with low visibility and where escape impediments were present (Table 6, Figure 6). Presence of scat by itself, on the other hand, did not trigger any changes in impala herd size (Table 5).

Table 5 Influence of elephant impact and scat treatment on the size of herds visiting the experimental plots for impala, warthog and rhino.

Experimental treatment	***Impala***	***Warthog***	***Rhino***
Elephant Impact	$13.56_{(4)}^{**}$	5.93	2.76
Scat	$0.50_{(2)}$	0.16	0.01
Elephant Impact × Scat	$11.34_{(4)*}$	2.23	2.90

The table shows test statistics (χ^2 values) with degrees of freedom in parenthesis and significance levels (°, p<0.1; *, p<0.05; **, p<0.01; ***, p<0.001).

Table 6 Effect sizes of elephant impact and scat treatment on size of impala herds visiting the experimental plots.

	Estimate	***SE***	***z***	***p***
Intercept (C)	1.33	0.29	4.65	0.000
EI	0.59	0.37	1.58	0.115
S	0.04	0.29	0.15	0.884
DV	-0.22	0.34	-0.66	0.512
DV&EI	-1.10	0.48	-2.27	0.023*
C × Scat	0.16	0.34	0.49	0.627
EI × Scat	-0.47	0.45	-1.03	0.302
S × Scat	-0.62	0.41	-1.49	0.136
DV × Scat	0.53	0.41	1.29	0.198
DV&EI × Scat	0.59	0.60	0.99	0.325

The table shows BAM test statistics (Estimate, standard error (SE), z and p values) with significance levels (°, p<0.1; *, p<0.05; **, p<0.01; ***, p<0.001).

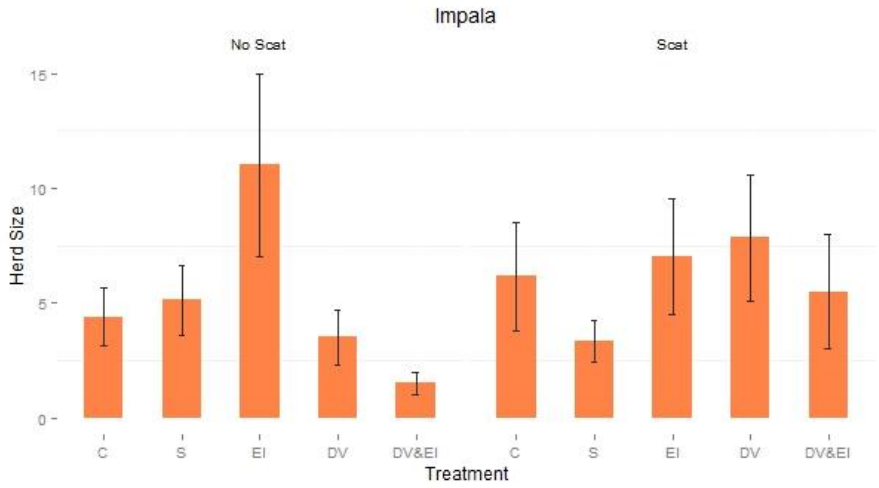

Figure 6 Impala (top) and warthog (bottom) herd size on the different experimental plots. Bars show average number of herds visiting plots of different treatments. Error bars reflect standard errors.

Occupancy

Habitat characteristics and scat did not influence the time impala and warthog spent at individual plots ($\chi^2 \leq 4.23$, $p \geq 0.38$ for impala and $\chi^2 \leq 1.79$, $p \geq 0.68$ for warthog). However, mimicked elephant impact had an effect on the amount of time rhino herds spend on individual plots ($\chi^2 = 13.83$, $p = 0.008$). A negative effect size of treatments with reduced visibility, escape impediments, or combination of both, on rhino occupancy was observed ($-0.89 < t < 1.54$, $0.383 > p > 0.135$), however the effect sizes did not differ from 0.

The effect of daytime

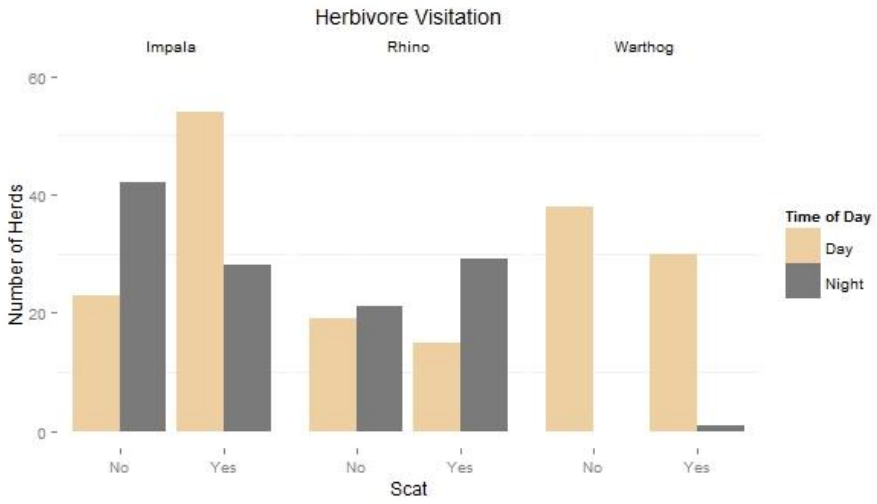

Figure 7 Total number of herbivore herds visiting experimental plots during day/night with or without presence of scat.

When taking time of day into account, it is clear that impala daily visitation patterns changed when adding scat (Figure 7). Without scat, more herds visit the plots at night, while this pattern reversed when scat was added. Visitation of rhino herds was a little higher at night, regardless of presence or absence of scat. Since warthog visitation at night was basically zero (Fig 6), it was excluded from further analysis.

Importantly, the effect of experimental treatments on impala visitation, but not herd size or occupancy, was highly dependent on time of day (significant interaction Experimental Treatment × Time of Day, Table 7). In contrast to impala, rhino showed no differences in response to experimental treatments during the distinct times of day (no significant fixed effects or interaction, Table 7).

Table 7 Influence of experimental treatment and time of day on the visitation, occupancy and herd size of impala and rhino (analysed with the Time of Day Model).

	Visitation		**Occupancy**		**Herd Size**	
	Impala	***Rhino***	***Impala***	***Rhino***	***Impala***	***Rhino***
Exp. Treatment	$46.11_{(9)}^{***}$	$8.43_{(9)}$	$15.77_{(9)}^{\circ}$	$14.99_{(9)}^{\circ}$	$26.74_{(9)}^{**}$	$5.24_{(9)}$
Time of Day	$0.49_{(1)}$	$1.51_{(1)}$	$1.33_{(1)}$	$0.48_{(1)}$	$4.45_{(1)}^{*}$	$0.01_{(1)}$
Exp. Treatment × Time of Day	$26.27_{(9)}^{**}$	$3.85_{(9)}$	$10.02_{(9)}$	$5.71_{(8)}$	$8.71_{(9)}$	$3.58_{(8)}$

The table shows test statistics (χ^2 values) with degrees of freedom in parenthesis and significance levels (°, p<0.1; *, p<0.05; **, p<0.01; ***, p<0.001).

Visitation

During the night time, impala showed a strong negative response to scat and habitat characteristics combined. In general, visitation during the night decreased (Fig 8).

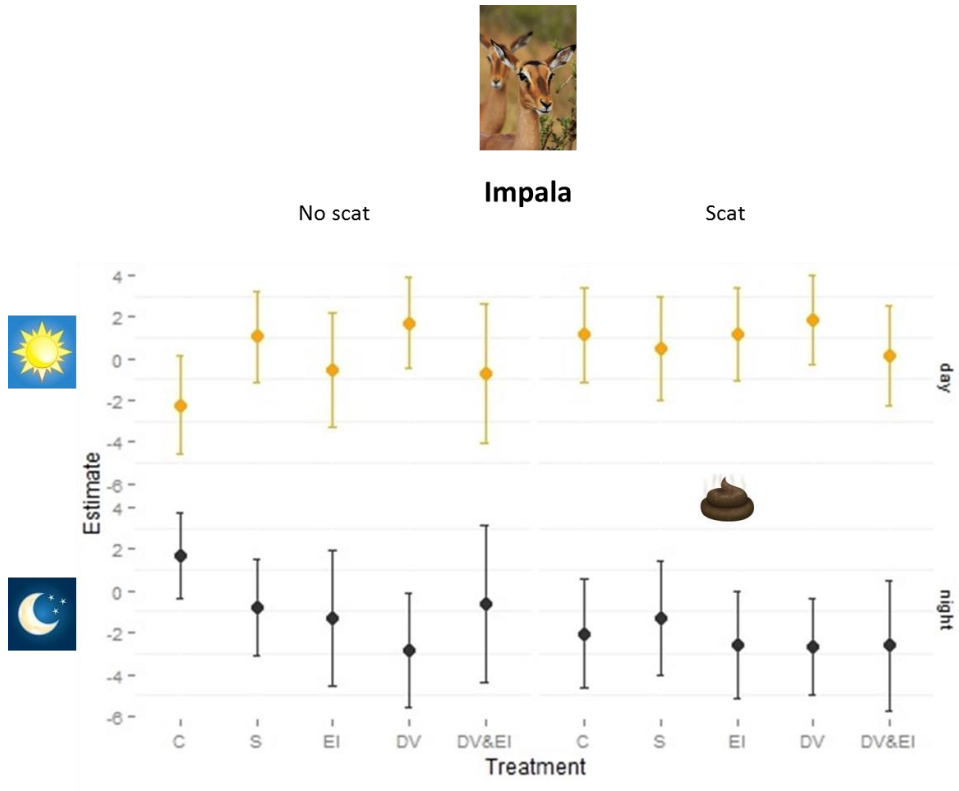

Figure 8 Model estimates with 95% confidence intervals for impala visitation in absence and presence of scat, during day and night.

While more herds visited plot with reduced visibility during the day, they avoided it during the night, regardless of scat presence. Interestingly, fewer impala herds visited escape impediment plots, but only at night and when scat was present. Also, at night without scat present, more impala visited control plots than other treatment plots, but visitation to control plots decreased to the level of treatments plots during the scat week (Table 8).

Table 8 Effect sizes of experimental treatment and time of day on visitation of impala and rhino herds. Effect sizes are given relative to the intercept.

Experimental Treatment	***Time of Day***	***Estimate***	***Error***	***z***	***p***
Intercept (C ns)	Day	-2.22	0.84	-2.68	0.007
C s		1.14	0.82	1.40	0.162
EI ns		-0.56	0.98	-0.57	0.568
EI s		1.14	0.79	1.44	0.151
S ns		1.05	0.77	1.37	0.172
S s		0.50	0.88	0.58	0.565
DV ns		1.71	0.78	2.19	0.028*
DV s		1.88	0.76	2.47	0.014*
DVEI ns		-0.74	1.18	-0.63	0.532
DVEI s		0.17	0.85	0.20	0.843

Intercept (C ns)	Night	1.71	0.74	2.32	0.021*
C s		-2.04	0.93	-2.21	0.027*
EI ns		-1.30	1.15	-1.13	0.259
EI s		-2.58	0.90	-2.86	0.004**
S ns		-0.81	0.83	-0.98	0.329
S s		-1.30	0.96	-1.35	0.177
DV ns		-2.80	0.97	-2.88	0.004**
DV s		-2.66	0.82	-3.24	0.001**
DVEI ns		-0.61	1.33	-0.46	0.649
DVEI s		-2.62	1.10	-2.38	0.017*

The table shows BAM test statistics (Estimate, standard error (SE), z and p values) with significance levels (°, p<0.1; *, p<0.05; **, p<0.01; ***, p<0.001). Significant estimates are shown in bold.

Herd size

Time was day influenced the size of impala herds visiting experimental plots but did not change the effect of experimental treatments (Table 7). During the night, herds of impala visiting treatment plots were smaller (z=-2.277, p=0.023). Rhino group size did not differ between different times of day (Table 7).

Occupancy

Time of day did not influence the time impala and rhino herds spent on the experimental plots (Table 7).

Discussion

This study shows that vulnerable prey species, impala and warthog, respond to fine-scale risk by avoiding elephant-induced coarse woody debris. However, the response of impala is strongly dependent on time of day and presence of scat. Impala selected for closed habitat with no CWD during the day, but selected against it at night time. Furthermore, it avoided plots with CWD only at night and in presence of scat, which highlights the importance of immediate predation risk and time of day on prey response. While warthog was inactive at night, it strongly responded to both habitat and within-habitat scale risk during the day. It avoided treatment plots with woody cover, escape impediments or both. Rhino, on the other hand, avoided lawn edges, but not escape impediments, and did not respond to scat, suggesting that the megaherbivore stays unaffected by manipulated predation risk.

Time of day affected impala's response to habitat scale predation risk, defined in terms of high woody cover. During daylight, more impala herds used plots with no escape impediments. As a mixed feeder, impala can feed on woody vegetation (pers. obs.) and use cover as a benefit to escape from chase predators (Scheel 1993). At night, however, impala shifted their habitat use dramatically, as they avoided the closed plots. Darkness may further decrease visibility and offer concealment for ambush predators (e.g. lions and leopards). This confirms previous findings that impala stays in open areas of short grasses at night where it can better detect the approaching danger (Caro 2005, Burkepile, Burns et al. 2013, Ford, Goheen et al. 2014). Interestingly, however, my results show that fine-scale risk, in the form of escape impediments, may counterbalance this effect of habitat openness. Generally, impala and warthog avoided plots where coarse woody debris was added. Impact of debris on perceived predation risk has already been described in studies from temperate systems, recognizing red deer avoidance of CWD as a response to fine scale predation risk (Halofsky and Ripple 2008, Kuijper, de Kleine et al. 2013). My results support these findings, suggesting that elephant-induced CWD increases fine-scale predation risk as perceived by impala and warthog. However, in addition to the previous studies, I show that response to CWD depended on the presence of immediate predation risk and the time of day. Impala perceived CWD as risky only at night and when scat was present. Moreover, by reducing the visitation of control plot at night during the scat treatment, I suggest impala responded to scat beyond individual treatment plots. At night, impala perceived the entire experimental site (grazing lawn) risky when a predator cue was present. Time of day and olfactory cues thus had a strong interactive effect in this study, generating the highest fine-scale predation risk for vulnerable prey species. Moreover, I show that impala use contrasting risk cues at habitat and within-habitat scale; during night, they use the open sites but avoid them if escape impediments and scat are present.

Impala's response to increased predation risk was recognized by the size of herds as well. Herds were smallest at plots with reduced visibility and escape impediments (DV&EI). Knowing that aggregation in large herds brings at least two important benefits; i)

probability of an individual being caught and killed decreases with increased group size (dilution effect) and ii) more animals provide more eyes for predator detection (many eyes effect), animal should be less susceptible to predation when living in a large herd (Lima and Dill 1990, Caro 2005, Favreau, Pays et al. 2013). However, the probability of attack is determined both by chance of prey encounter and the predator's decision to hunt upon encountering. Fitzgibbon and Lazarus (1995) and Creel and Creel (2002) showed that large herds will be more likely attacked once located. Grouping in smaller herds may thus be beneficial, but only in closed habitats where small groups have less chance to get noticed than larger ones (Creel and Winnie Jr 2005). Fewer animals sharing the space around woody cover could also bring advantages for foraging. Less individuals feeding from the same bush face lower intraspecific competition for food, benefiting herd as a whole (du Toit and Yetman 2005).I suggest impala thus responded to risk with forming smaller herds. Impala herds were smaller during the night time as well. Considering the fact that predation risk increases at that time of day, smaller groups should form only close to cover (as discussed above), but I did not find this in this study. However, an observer bias for night herd size data may exist. Camera traps were using infrared light that enabled night vision. The quality of night footage was sufficient for recognition of individuals in the 5 × 5 m experimental plots, but decreased when animals appeared at further distances. With only a part of a herd being visible clearly and the rest being recognized only by the eye reflections, estimating the size of the whole herd was difficult. I thus suggest the results of herd size for night time to be interpreted with caution.

Warthog was completely absent from grazing lawns during the night, which confirms previous studies showing that warthog is a highly diurnal animal (Somers 1997). Warthog uses burrows to escape from predation and avoid periods of high predation risk (White and Cameron 2009). Since most predators are active at night, staying in burrows can be considered as an important antipredator strategy. At day, warthog actively used the grazing lawns but avoided CWD and woody cover, showing a strong response to both habitat and within habitat scale predation risk. However, unlike impala, I suggest warthog perceived CWD not only as escape impediment but also as visibility obstruction. First, impala could see over the escape impediments while standing and warthog could not; visibility at impala level (100 cm) was higher than visibility at warthog level (50 cm), measured above and approximately at the level of escape impediments (with a height of approximately 50 cm), respectively. Second, less warthog groups visited the plot with woody cover but no escape impediments, which is opposite of impala. Warthog's avoidance of plots with poor visibility can be explained by the fact that its main predator is lion, a sit-and-wait predator that uses cover in its benefit (Owen-Smith and Mills 2008). Impala, on the other hand, is a preferred prey of a wider range of predators (lion, leopard, wild dog) that hunt both in the open and closed habitats, making different habitats equally risky (Thaker, Vanak et al. 2010). In addition, impala is a mixed feeder, recognizing woody vegetation also as forage opportunity, especially in the dry season (Scheel 1993, du Toit and Yetman 2005).

Contrary to response of vulnerable prey species, rhino did not respond to manipulations in predation risk (addition of escape impediments and/or scat). However, it still avoided plots

on the edge of the grazing lawn (DV and DV&EI). The precise reason for such response remains unclear. Even though the results from statistical analysis did not show any differences in food availability among treatment plots, there might have been less grazing material at closed plots due to i) high proportion of exposed ground under the overshadowing bushes and ii) increased amount of leaf litter produced by the surrounding woody vegetation (pers. obs.). The reduced cover of grasses could deter rhino, resulting in its avoidance of lawn edges. When accounting for time of day, the effect of treatment on rhino visitation disappears. Though, this might result from low sample size, giving an average of less than one herd per treatment plot under distinct times of day. Since rhino avoided lawn edges but not plots with CWD only, I suggest rhino did not recognize increased fine-scale predation risk. This supports the idea that the megaherbivore does not perceive risk (Owen-Smith 1988). The conclusion has been made through Owen-Smith's personal observations, excluding experimental tests of megaherbivore response to predation risk. My study, on the other hand, provides unique experimental evidence of rhino's lack of response to predation risk cues.

Even though several different studies advocate vigilance as a measurement of herbivore response to predation risk (Fitzgibbon and Lazarus 1995, Hunter and Skinner 1998, Laundre, Hernandez et al. 2001, Valeix, Loveridge et al. 2009), it was not considered as one of the response variables in this study. Inspecting the surroundings does not necessarily suggest looking for predators, especially when animals live in groups, or herds. Social ungulates rely largely on their sight for communication, finding food and coordination with the rest of the group members. Levels of vigilance differ between age and sex groups but may besides recognizing predation risk essentially indicate competition (for mates, food or territory), social factors (maintaining hierarchy) or foraging efforts (finding most optimal forage) (Caro 2005). Favreau et al. (2013) recommends a careful approach towards using vigilance as a proxy of predation risk in social species (such as impala in this case) since both social and predator cues directly affect the gregariousness of individuals. Considering those suggestions and the fact that my experiment did not allow differentiation between the underlying reasons for vigilance, this behaviour was considered as a poor measure of response to predation risk and omitted from the analysis.

Based on the results discussed above, I suggest elephants mediate both habitat scale and within habitat scale predation risk, but only for vulnerable herbivores. However, the influence of elephants on habitat scale risk needs further attention. Testing habitat scale risk was limited to grazing lawns, using only differences in woody cover to distinguish between different "habitats". That enabled standardized conditions in terms of resource accessibility; however it only provided insight to grazing lawns as individual functional units in savannah ecosystem. For a more comprehensive approach, a comparison of herbivore response between different savannah habitats could be made. It is important to note that elephants affect different plant communities differently and the response to predation risk may thus also be different.

Running the experiment on grazing lawns allowed control for food availability and quality. Though, I run the experiment during the dry season, which is the period that grasses are no longer growing and instead start to dry out (Figure 1). Consequently, the productivity of lawns during my experiment was very low (see Fig 2) and likely offered only limited resources to grazers. From previous work we know that grazing ungulates like zebra and wildebeest stop using grazing lawns in the dry season and rather move to areas with taller grasses (Arsenault and Owen-Smith 2011). My data indeed confirmed a very low visitation of herds of these ungulate species to the experimental sites (Table 1). The herbivores that did use the lawns were either mixed feeders, like impala, that can feed on woody vegetation at the edge of the lawn (du Toit and Yetman 2005, pers. obs.), or species that are specialized grazers of short grasses, like rhino and warthog (Cromsigt and Olff 2008). Due to its morphological adaptations, i.e. "…wide mouth and lip-plucking grazing technique" (Arsenault and Owen-Smith 2011), rhino can continue utilizing grazing lawns during the dry season, when grass height drops under 5 cm (Perrin and Brereton-Stiles 1999) but can also start feeding on taller, less nutritious grasses. Additionally, rhino utilizes grazing lawns for mineral intake. A particularly limiting element for large grazers like rhino is sodium (Clauss, Castell et al. 2007) and grazing lawn grasses may have particularly high concentration of Sodium in their leaves (Veldhuis, Howison et al. 2014). In addition, exposed ground on grazing lawns during the dry season may serve for acquisition of essential minerals, such as sodium. Smaller grazers such as warthog cannot gain enough energy from coarse, fibrous vegetation and are restricted to feed on nutritious grasses, found on the lawns (Sinclair, Mduma et al. 2003, Cromsigt and Olff 2008). With its unique mouth morphology and feeding on bent knees, warthog can not only consume shortest grass shoots but often dig out the equally rich roots as well (Botha and Stock 2005). Thus grazing lawns stay a primary source of food for warthog even during the dry season.

Low food availability during my experiment has another important consequence for my study. According to the "risk allocation hypothesis", herbivores limited by resources will reduce their response to predation risk (Lima and Dill 1990). Since herbivores showed a clear response to increased predation risk during the dry season, I assume the presented results are quite robust. Should the experiment be repeated in the wet season, I expect herbivore response to be even stronger.

My thesis fully supports the prediction that increased levels of predation risk only affect vulnerable herbivore species. Moreover, the responses are highly influenced by presence of immediate predation risk and time of day. Impala perceived elephant induced vegetation modifications risky only when predator is actively hunting in the vicinity, i.e. when the cues from the environment are suggesting a high chance of having to escape from a predator at that particular moment. The results from the second, Time of Day model, provide a better insight to the findings from the Scat model, but essentially lead to the same conclusion. By changing the openness of the habitats and adding CWD within those habitats, elephants have an important influence on predation risk. Importantly, my thesis indicates that these elephant impacts may in fact have contrasting effects on perceived risk, where opening the habitat reduces perceived risk but adding CWD increases it.

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Bibliography

Apfelbach, R., C. D. Blanchard, R. J. Blanchard, R. A. Hayes and I. S. McGregor (2005)."The effects of predator odors in mammalian prey species: a review of field and laboratory studies." Neurosci Biobehav Rev 29(8): 1123-1144.

Archibald, S. (2008). "African Grazing Lawns—How Fire, Rainfall, and Grazer Numbers Interact to Affect Grass Community States." The Journal of Wildlife Management 72(2): 492-501.

Arsenault, R. and N. Owen-Smith (2011). "Competition and coexistence among short-grass grazers in the Hluhluwe-iMfolozi Park, South Africa." Canadian Journal of Zoology 89(10): 900-907.

Bates, D., M. Maechler, B. Bolker and S. Walker (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7, http://CRAN.R-project.org/package=lme4.

Botha, M. S. and W. D. Stock (2005) "Stable isotope composition of faeces as an indicator of seasonal diet selection in wild herbivores in southern Africa : research letter." 101, p.371-374.

Boundja, R. P. and J. J. Midgley (2010). "Patterns of elephant impact on woody plants in the Hluhluwe-Imfolozi park, Kwazulu-Natal, South Africa." African Journal of Ecology 48(1): 206-214.

Brown, J. S., J. W. Laundre and M. Gurung (1999). "The ecology of fear: Optimal foraging, game theory, and trophic interactions." Journal of Mammalogy 80(2): 385-399.

Burkepile, D. E., C. E. Burns, C. J. Tambling, E. Amendola, G. M. Buis, N. Govender, V. Nelson, D. I. Thompson, A. D. Zinn and M. D. Smith (2013). "Habitat selection by large herbivores in a southern African savanna: the relative roles of bottom-up and top-down forces." Ecosphere 4(11).

Caro, T. (2005). Antipredator Defenses in Birds and Mammals. Chicago, The University of Chicago Press.

Clauss, M., J. C. Castell, E. Kienzle, P. Schramel, E. S. Dierenfeld, E. J. Flach, O. Behlert, W. J. Streich, J. Hummel and J. M. Hatt (2007). "Mineral absorption in the black rhinoceros (Diceros bicornis) as compared with the domestic horse." Journal of Animal Physiology and Animal Nutrition 91(5-6): 193-204.

Creel, S. and N. M. Creel (2002). The African Wild Dog: Behaviour, Ecology and Conservation. Princeton, New Jersey, Princeton University Press.

Creel, S. and J. A. Winnie Jr (2005). "Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves." Animal Behaviour 69(5): 1181-1189.

Cromsigt, J. P. G. M. and H. Olff (2008). "Dynamics of grazing lawn formation: an experimental test of the role of scale-dependent processes." Oikos 117(10): 1444-1452.

du Toit, J. T. and C. A. Yetman (2005). "Effects of body size on the diurnal activity budgets of African browsing ruminants." Oecologia 143(2): 317-325.

Favreau, F. R., O. Pays, A. W. Goldizen and H. Fritz (2013). "Short-Term Behavioural Responses of Impalas in Simulated Antipredator and Social Contexts." Plos One 8(12).

Fitzgibbon, C. D. and J. Lazarus (1995). Antipredator behavior of Serengeti ungulates: Individual differences and population consequences.

Ford, A. T., J. R. Goheen, T. O. Otieno, L. Bidner, L. A. Isbell, T. M. Palmer, D. Ward, R. Woodroffe and R. M. Pringle (2014). "Large carnivores make savanna tree communities less thorny." Science 346(6207): 346-349.
Guldemond, R. and R. Van Aarde (2008). "A meta-analysis of the impact of African elephants on savanna vegetation." Journal of Wildlife Management 72(4): 892-899.
Halofsky, J. S. and W. J. Ripple (2008). "Fine-scale predation risk on elk after wolf reintroduction in Yellowstone National Park, USA." Oecologia 155(4): 869-877.
Haynes, G. (2012). "Elephants (and extinct relatives) as earth-movers and ecosystem engineers." Geomorphology 157: 99-107.
Hopcraft, J. G. C., H. Olff and A. R. E. Sinclair (2010). "Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas." Trends in Ecology & Evolution 25(2): 119-128.
Hunter, L. T. B. and J. D. Skinner (1998). "Vigilance behaviour in African ungulates: The role of predation pressure." Behaviour 135: 195-211.
Jones, C. G., J. H. Lawton and M. Shachak (1994). "Organisms as ecosystem engineers." Oikos 69(3): 373-386.
Jones, C. G., J. H. Lawton and M. Shachak (1997). "Positive and negative effects of organisms as physical ecosystem engineers." Ecology 78(7): 1946-1957.
Kerley, G. I. H. and M. Landman (2006). "The impacts of elephants on biodiversity in the Eastern Cape subtropical thickets." South African Journal of Science 102(9-10): 395-402.
Kuijper, D. P. J., C. de Kleine, M. Churski, P. van Hooft, J. Bubnicki and B. Jędrzejewska (2013). "Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland." Ecography 36(12): 1263-1275.
Kuijper, D. P. J., M. Verwijmeren, M. Churski, A. Zbyryt, K. Schmidt, B. Jędrzejewska and C. Smit (2014). "What Cues Do Ungulates Use to Assess Predation Risk in Dense Temperate Forests?" PLoS ONE 9(1): e84607.
Laundre, J. W., L. Hernandez and K. B. Altendorf (2001). "Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA." Canadian Journal of Zoology-Revue Canadienne De Zoologie 79(8): 1401-1409.
Laws, R. M. (1970). "Elephants as agents of habitat and landscape change in east-africa." Oikos 21(1): 1-&.
Lima, S. L. and L. M. Dill (1990). "Behavioral decisions made under the risk of predation - a review and prospectus." Canadian Journal of Zoology-Revue Canadienne De Zoologie 68(4): 619-640.
McNaughton, S. J. (1984). "Grazing lawns - animals in herds, plant form, and coevolution." American Naturalist 124(6): 863-886.
Mysterud, A. and E. Østbye (1999). "Cover as a Habitat Element for Temperate Ungulates: Effects on Habitat Selection and Demography." Wildlife Society Bulletin 27(2): 385-394.
Nolte, D., J. R. Mason, G. Epple, E. Aronov and D. Campbell (1994). "Why are predator urines aversive to prey?" Journal of Chemical Ecology 20(7): 1505-1516.
Owen-Smith, N. and M. G. L. Mills (2008). "Predator–prey size relationships in an African large-mammal food web." Journal of Animal Ecology 77(1): 173-183.
Owen-Smith, R. N. (1988). Megaherbivores, Cambridge University Press.
Owensmith, R. N. (1989). "Megafaunal extinctions - the conservation message from 11,000 years bp." Conservation Biology 3(4): 405-412.
Perrin, M. R. and R. Brereton-Stiles (1999) "Habitat use and feeding behaviour of the buffalo and the white rhinoceros in the Hluhluwe-Umfolozi Game Reserve." 29, 72-80.

Ripple, W. J. and R. L. Beschta (2004). "Wolves and the ecology of fear: Can predation risk structure ecosystems?" Bioscience 54(8): 755-766.
Sankaran, M., D. J. Augustine and J. Ratnam (2013). "Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna." Journal of Ecology 101(6): 1389-1399.
Scheel, D. (1993). "Watching for lions in the grass - the usefulness of scanning and its effects during hunts." Animal Behaviour 46(4): 695-704.
Shannon, G., M. Thaker, A. T. Vanak, B. R. Page, R. Grant and R. Slotow (2011). "Relative Impacts of Elephant and Fire on Large Trees in a Savanna Ecosystem." Ecosystems 14(8): 1372-1381.
Sinclair, A. R. E., S. Mduma and J. S. Brashares (2003). "Patterns of predation in a diverse predator-prey system." Nature 425(6955): 288-290.
Somers, M. (1997). "Activity patterns and activity budgets of warthogs (Phacochoerus aethiopicus) in the Eastern Cape Province, South Africa." African Journal of Ecology 35(1): 73-79.
Tambling, C. J., L. Minnie, J. Adendorff and G. I. H. Kerley (2013). "Elephants facilitate impact of large predators on small ungulate prey species." Basic and Applied Ecology 14(8): 694-701.
Thaker, M., A. T. Vanak, C. R. Owen, M. B. Ogden, S. M. Niemann and R. Slotow (2010). "Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates." Ecology 92(2): 398-407.
Trinkel, M., N. Ferguson, A. Reid, C. Reid, M. Somers, L. Turelli, J. Graf, M. Szykman, D. Cooper, P. Haverman, G. Kastberger, C. Packer and R. Slotow (2008). "Translocating lions into an inbred lion population in the Hluhluwe-iMfolozi Park, South Africa." Animal Conservation 11(2): 138-143.
Trollope, W. S. W., L. A. Trollope, H. C. Biggs, D. Pienaar and A. L. F. Potgieter (1998). "Long-term changes in the woody vegetation of the Kruger National Park, with special reference to the effects of elephants and fire." Koedoe 41(2): 103-112.
Valeix, M., H. Fritz, S. Chamaille-Jammes, M. Bourgarel and F. Murindagomo (2008). "Fluctuations in abundance of large herbivore populations: insights into the influence of dry season rainfall and elephant numbers from long-lterm data." Animal Conservation 11(5): 391-400.
Valeix, M., H. Fritz, R. Sabatier, F. Murindagomo, D. Cumming and P. Duncan (2011). "Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna." Biological Conservation 144(2): 902-912.
Valeix, M., A. J. Loveridge, S. Chamaille-Jammes, Z. Davidson, F. Murindagomo, H. Fritz and D. W. Macdonald (2009). "Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use." Ecology 90(1): 23-30.
Veldhuis, M. P., R. A. Howison, R. W. Fokkema, E. Tielens and H. Olff (2014). "A novel mechanism for grazing lawn formation: large herbivore-induced modification of the plant–soil water balance." Journal of Ecology 102(6): 1506-1517.
Vos, I. (2010). Spatial Heterogeneity of Resources. Master, Utrecht University.
Waldram, M., W. Bond and W. Stock (2008). "Ecological Engineering by a Mega-Grazer: White Rhino Impacts on a South African Savanna." Ecosystems 11(1): 101-112.
White, A. M. and E. Z. Cameron (2009). "Communal nesting is unrelated to burrow availability in the common warthog." Animal Behaviour 77(1): 87-94.
Wright, J. P. and C. G. Jones (2004). "Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity." Ecology 85(8): 2071-2081.

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